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THE EDAPHIC FACTOR IN NARROW ENDEMISM. I. THE NATURE OF ENVIRONMENTAL INFLUENCES

Herbert L. Mason

There are three aspects to the dynamics of any problem involving the geographic distribution of plants. First there is the environment, represented by a series of intensity spans of the various environmental factors or by conditions or sequences of conditions of these factors. Secondly there are the physiological reactions of the individual plant that function within limits of tolerance for the conditions prevailing within the environment. Thirdly there are the genetic processes that operate to fix tolerance ranges of and give character to the individual, to control the variability of the population, and to give rise to new individuals preadapted to this environment or endowed with the potentiality for extending the area of the species. The interaction of these three forces determines the area occupied by any group of plants and no other force, except as it may influence either directly or indirectly the interaction of these three, can in any way affect the distributional pattern of the population.

The functioning of all plants is conditioned by environmental factors acting to control physiological processes. The relationship between environment and physiology in each individual case is probably genetically fixed as to the nature and span of the tolerances concerned. The fixation of tolerance spans may result from any of the isolating mechanisms of genetics that function to elaborate plants over the available habitats, each species or population being restricted to the area of the environmental conditions to which the tolerances of its component members are suited. These dynamics apply to all plants, hence all plants are restricted in range. Restriction in range is purely relative and is always related to environmental factors through physiological and genetic processes.

When the literature dealing with the subject of endemism is reviewed in the light of these ideas it becomes evident that there is much misunderstanding of the problems that relate to species of highly restricted range. Most of the difficulties result from an attempt to apply abstract ideas in the role of factors in cause-and-effect relationships. There are frequently encountered such terms as "age factor," meaning either age of species or age of land mass; "size factor," inferring size of land mass; "isolation," as a causal factor rather than as a term descriptive of a situation in which the real causes operate; and "historical factor," used in a vague sense to imply causal relationships bound often to unknown events of the past. I shall return later to a discussion of

these abstractions. For the present it will be sufficient to point out that none of these concepts can be applied with significance to problems of physiological reactions of the individuals of the population or to the genetic processes that control a population. They can therefore have no influence in the restriction of area of any species of plant. The many difficult problems relating to endemism can never be solved by continuing to apply abstract ideas toward their solution. Endemic species, like every other species of plant, are made up of individuals that are functioning organisms. Their physiological reactions operate under the influence of environmental conditions. Their precise nature is the result of genetic processes. The general dynamics applying to problems of their geographic distribution must therefore be the same as those applying to all plants. Since there is so much misunderstanding of these problems, I deem it pertinent, before entering upon my subject, to discuss very briefly what I presume to be the nature of the roles of the environment, of the physiology of the individual of the population, and of population genetics, as they operate in vegetation dynamics. Although certain aspects of broad endemism are herein discussed, it should be borne in mind that the main thesis of this paper is the highly restricted patterns of distribution.

The Nature of Environmental Relations

The geographic area occupied by any group of plants is controlled by definite intensity spans or rhythmic patterns of certain conditions of environmental factors. Climatic factors in any given region are most inclusive in their scope of control. They may function within a pattern laid down by diurnal and seasonal rhythm. The nature and sequence of this rhythm may at times be a limiting factor to the occurrence of certain species of plants and may be equal in significance to the extremes (8, 10) of the intensity span of any environmental factor in its function of determining and controlling the periphery of the area that any species can occupy. Practically the entire range of normal climatic situations over the surface of the earth provides suitable habitats for plant populations, given an adequate edaphic setting.

In any given region the various aspects of the edaphic factor operate wholly within the conditions superimposed by climate. They may be relatively stable in their occurrence and span of intensity, or they may fluctuate as a direct result of some chance climatic sequence of events or with the rhythm of climatic events, or their fluctuation may be imposed by biotic factors or diastrophic processes. Here again, where the fluctuation is rhythmic, the rhythm may function as a limiting factor much as does the rhythm of climatic events. An example of such a rhythm is the seasonal fluctuation in the position of the water table, or the seasonal fluctuation of the soil-moisture content in certain arid regions, or the

seasonal sequence of salinity or of hydrogen-ion concentration in certain soil solutions. Almost the whole enormous range of edaphic situations provides suitable habitats for some plant populations.

The biotic factor, being the result of the functioning of organisms, is in itself subject to the whole gamut of environmental factors, hence its various aspects operate within conditions prescribed by climatic and edaphic factors. Often the precise biotic effect may result from the regular coincidence of one phase of a life cycle with a certain phase of the life cycle of another organism upon which it depends or which it may influence. The yucca moth must emerge at the time that the yucca is flowering or no pollination will result. Here is a case of the necessity for the coincidence of two ontogenetic rhythms to insure proper functioning. Any factor that disturbs either of these rhythmic sequences to the extent that these two ontogenetic phases no longer coincide, would cause the yucca to lose its capacity to reproduce. There are many biotic environments that possess their special floras; frequently they consist of populations of single species and they often involve various aspects of parasitism and hemiparasitism.

It will thus be clear that the problems of environmental factors in their conditioning reactions on physiological processes of plants are not always simple problems of presence or absence, nor are they always simple problems of intensity or the gradient between extremes. They may involve the coincidence of many rhythmic sequences of fluctuating presence and absence, or fluctuating intensities with fluctuating physiological demands, or rhythmic sequences in the ontogeny of the plant. Often they operate to condition one another and may, in so doing, alter the physiological response. Most significant to problems of plant geography is the fact that environmental conditions occupy area independently of whether any precise condition may or may not influence a particular organism.

THE PHYSIOLOGY OF THE INDIVIDUAL

The response of the organism to the conditions of its environment may be expressed in terms of the principle of limiting factors (8), and the theory of tolerance (7) or the theory of physiological limits (3); such relationships, insofar as they are inherent within the species, are subject to the laws of evolution and genetics. Within the species or population, the range of variation of the capacity to tolerate various aspects of the environmental factors is the direct result of the genetic diversity of the species or population in question (9). The functioning of all plants, regardless of their degree of geographic restriction or the age of the species, is conditioned by environmental factors acting or interacting to control physiological processes. Just as there are rhythmic aspects in many types of environmental factors, there are rhyth–

mic aspects in the diurnal and seasonal phases of the plant's physiology as well as in the seasonal aspects of its ontogeny. Each phase of the rhythm of ontogeny or the rhythm of physiology is controlled by its own span or sequence of environmental conditions, and one phase of the ontogeny or physiology may make different demands upon the environment than another. Thus, some plants require a significant drop in temperature at night; others require a reasonably sustained temperature. Some plants come into flower under the influence of a seasonal sequence of rising temperatures and sustained water supply, while others, such as the summer annuals of the California foothills, appear to require a seasonal sequence of rising temperatures and decreasing water supply. During the occasional season when water supply is sustained, these plants spend most of their energy in developing foliage, and they produce few flowers, or flowering may be seriously retarded seasonally. Owing to the great mortality of seedlings between germination and establishment in nature, one must conclude either that some physiological process has a very narrow span of tolerance for some factor of the environment, or that the coincidence of a physiological or ontogenetic rhythm with some aspect of seasonal rhythm of the environmental complex is under very fine adjustment. An example is the environmental condition that controls the establishment of seedlings of the highly restricted endemic Monterey cypress, *Cupressus macrocarpa* Don, in its native habitat. In a normal year the moisture content of the surface soil recedes very rapidly at the end of the rainy season. If the growth of the taproot of the seedling is able to keep pace with the recession of the soil moisture the seedling will become established. If not, the seedling dries up and dies. Here an essential coincidence between two rhythmic cycles is usually out of adjustment and normally results in no establishment of seedlings. It is only occasionally that conditions are favorable for the establishment of seedlings of this species in its native habitat. Favorable conditions may result from late rain or a cool spring, and during such occasional years the establishment of seedlings is abundant. It is well to point out here that this is a problem of the relation of a species to its environment involving the species as it is constituted genetically and physiologically today, meeting environmental conditions as they prevail today. Given a plant so constituted and an environment so characterized, the age and source of the species to which it belongs, or the incidents in the history of the species, have no bearing on the problem of how the plant reacts to the conditions of its environment except as conditions and incidents of the past, reacting on the developing species population, may have influenced the genetic processes responsible for the present constitution of the plant.

The physiological processes of the plant, whether they involve nutrition, respiration, growth or reproduction, operate under the

influence or sanction of environmental conditions. The environ-
ment functions to control the physiological processes, and, be-
cause the conditions of the environment occupy area, they circum-
scribe the area in which the process can function. Thus the dy-
namics of the physiology of the individuals of a population
become linked with the dynamics of the environment to control
the area the population can occupy.

The Role of the Genetics of the Individual and of the Population

Genetics, by whatever mechanism it may operate, in each
individual case functions to set the capacity of the plant to toler-
ate the conditions of the environment. Once the zygote is formed,
the role of genetics, so far as the new individual and its charac-
teristics are concerned, is ended. This however is not the case
with the population. The population is continuous beyond the
life span of the individual. Its continuity results from the repro-
ductive process among individuals which inevitably sets in motion
the mechanics of population genetics. Each of these aspects
of genetics plays an important role in the dynamics of plant
geography.

There is enough evidence now at hand to justify the general
conclusion that the relationship between function and its condi-
tioning environmental factors is genetically fixed within each in-
dividual plant. The tolerance span of the individual is but an in-
crement of the total span of variation that characterizes the
species or the population with respect to any particular function
and its conditioning environmental factors. Furthermore, the fix-
ing of the tolerance span of the individual, or of the population or
of the species, may result from any of the isolating mechanisms
operating in the genetics of plants. Out of the diverse mass of seed
presented to it, the environment is able to select only those indi-
viduals that are preadapted by their tolerance spans to become
established and survive under the conditions prevailing in the area
into which the seeds chance to fall. This repeated selection,
generation after generation, tends to fix the form and the physi-
ological capacity of the individuals of the species and to control
the range of genetic diversity of the population that may occupy
an area characterized by any given set of environmental condi-
tions. It is akin to what Turesson (14) termed a "genotypical
response of the plant species to its habitat." It results in a
genetic race thoroughly in adjustment with the pattern of inter-
action between the various factors of the environment and the
physiological processes of the plant that govern germination,
establishment, and the functioning of the mature individual. It is
through these processes that the species is enabled to persist in
a given environment through the normal fluctuation of habitat
conditions. It is likewise through these processes of genetic

variation that individuals develop that are capable of extending the population into new habitats. Only in this way can a species overcome the great environmental diversity that otherwise would serve as a barrier to its migration. Many aspects of the edaphic environment do not migrate with climatic changes; these, therefore, stand as either selective agents or barriers imposed across the path of a migrating flora. Thus, extensive migration, even though it accompany a definite climatic environment in its shift, will probably result in considerable ecotypic differentiation and speciation, as well as in some extermination at various points in its course. To our thesis it is most important that the seed destined to survive in the new environment arrives already preadapted to the new conditions through the genetic phenomena that are inherent in the reproductive process. The new environment plays no part in this preadaptation.

Because of the nature of the usual reproductive process, every problem involving the geographic distribution of such plants must of necessity be concerned with the genetics of populations. The mechanics of population genetics have inherent in them the potentialities for inducing or restricting morphological and physiological variation in the population, as well as for initiating and pursuing the various processes leading to speciation that may function to elaborate the population over the available habitats. These mechanics owe their amplitude in any given environment to such things as the genetic diversity of the population, the nature and rate of mutations, gene infiltration, and the chromosomal phenomena that may alter the nature, arrangement, and quantity of genic materials entering the zygote, as well as to the selective influences of the conditions of the environment. Any of these phenomena may function to alter form and physiological responses of the individuals of the population and thus give rise to habitat types adapted to the particular environmental complex or complexes prevailing in the area. The population may operate wholly within its own genetic influence and become stabilized through random fixation, or it may be subject to frequent mutation or to gene infiltration that will function to keep it in a relatively unstable condition genetically. Whatever the situation may be, for purposes of plant geography it must be constantly borne in mind that the genetic phenomena involving the individual of the population, as well as the population as a whole, concern the physiological responses of individuals to the conditions of the environment and therefore have an important bearing on problems involved in the area the population can occupy.

Genetic diversity within the population may be expressed in terms of biotype number. At any given time biotype number in the population is the result of the interaction of genetic and physiological processes and environmental factors. This being the case, so far as the environmental relations are concerned, the

number of biotypes in an area is to be determined by environmen-
tal conditions and not by the size of the area. Aside from purely
environmental relations, the number of biotypes in an area is
subject to such genetic phenomena as chromosome aberrations,
gene infiltration, and random fixation. Thus, when conditions are
alike over a wide area and genetic phenomena relatively stable,
one might find few biotypes over the entire area. When great
environmental diversity prevails in a small area and genetic insta-
bility characterizes the population, there may be many biotypes
in a small area. On the other hand we may have, as Stebbins
(13) has pointed out, a definite correlation between restriction of
species and biotype depauperization. Here, in all probability,
there must also be a close relation between environmental con-
dition and adjusted tolerances resulting from biotype depauperi-
zation of the population. It must, however, be pointed out that
the phenomena reported by Stebbins may not always of necessity
be reflected in reduced size of area. It will be so only when toler-
ance spans are reduced along with biotype reduction, and the
conditions to which the adjustment is suited occupy smaller area.

This discussion of the relation of the organism and the species
population to its environment is pertinent to my subject because
it demonstrates that the variations possible in the interaction of
an enormously complex series of environmental factors with the
physiological mechanisms of plants under the influence of ordi-
nary genetic processes are sufficiently great to give rise to a plant
population with all of the peculiarities of minor speciation and
distribution pattern known to us today. It should be clear that
the populations of special environments result from genetic differ-
entiation. This is essentially the mechanism behind floristic
diversity, a condition that obviously is to be associated with en-
vironmental and genetic diversity in their effect on physiological
processes. The key to the problem is diversity. The greater the
environmental diversity the broader the selective powers of the
environment. It must follow that the greater the genetic diver-
sity, the more numerous will be the opportunities for the exercise
of environmental selection. The precise outline of the geo-
graphic occurrence of a species will be determined by the out-
lines of one or more increments of the pattern of environmental
diversity. The nature of the species will result from genetic
processes under the influence of environmental selection.

ENDEMISM, AREA AND GEOGRAPHIC RESTRICTION

For these reasons all plants are restricted in their geographic
area by environmental conditions, and, for these same reasons, all
plants are, in a sense, endemics. The area of their occurrences
is determined by precisely the same set of dynamics. It would
appear that endemism results from forces operating to limit or
restrict the area of all species, and that the nature of these forces

is the interplay or interaction of environmental factors on physio-
logical and genetic processes. The manifestation of restriction
may be in the form of a response to climatic, edaphic, or biotic
factors, or to any combination of these. There is evidence that
all of these, singly or in various combinations, have been responsi-
ble for some aspect of endemism. Endemism should not be bur-
dened with indefinable presumed freak distribution patterns, nor
should it be confined to highly restricted patterns of distribution.
When so treated it is set upon a plane where normal explanations
seem not to apply. It should be constantly borne in mind that the
dynamics of plant distribution are essentially the same or of the
same order for all plants, and that these dynamics may serve as
a pattern or framework upon which to build interpretations or
explanations of the many problems of either usual or unusual
distribution.

With this concept of endemism we have in no way altered the
problem; we have altered only the point of view. We still have
restricted endemism and broad endemism, old species and young
species, and all stages in between. We still must seek explana-
tions in terms of cause and effect. With this point of view, how-
ever, *area becomes subordinated to environmental condition. The area
is incidental to the condition and is significant only because the con-
dition occupies area.* Environmental diversity becomes the key to
floristic diversity, and the more precise patterns of distribution
must be involved with the more precise causes. In general, the
larger the area occupied by a species the more apt is its periphery
to be under the influence of a complex series of limiting factors.
These may operate differently in the various segments of the
periphery of the area of the species. The smaller the area occu-
pied by the species the fewer will be the factors concerned with
its restriction until, in certain highly restricted patterns of distri-
bution, a single limiting factor may suffice. Although this rela-
tionship is in general true, it obviously cannot be absolute because
it is perfectly possible for a single factor or a few factors to con-
trol fairly large areas or for small areas to be controlled by
several series of factors.

The causes behind any particular pattern of geographic distri-
bution of plants may be numerous and diverse. They must, how-
ever, be of the nature of conditioning factors to physiological
processes. Since their chief manifestation is a pattern of geo-
graphic distribution within an area, it follows that the causes must
be related to conditions that likewise occupy area independently
of the fact that plant species may be restricted by them. Of the
three aspects of the dynamics of plant geography, only that per-
taining to the environment independently occupies area. There-
fore we may conclude that causes behind any patterns of distri-
bution are intimately linked with the environment, and that the
distributional patterns are circumscribed by environmental con-

ditions.   It is the areal span of the environmental condition to which the plant is preadapted that determines the area that any species can occupy.   If the condition is local, the potential area of the species will be local; if the condition is widespread, the potential area of the species will be broad.   Likewise, if the area of the condition is continuous, the potential area of the species is continuous; if the condition is discontinuous, the potential area will be discontinuous.   This does not mean that all plants occupy all of their potential area, but it does mean that all plants have a potential area characterized by a given set of environmental conditions occurring in a definite span of intensity and often in definite rhythmic sequences.   The plant, having the capacity to tolerate a particular set of environmental conditions, will—unless effectual barriers exist—soon occupy all of its potential area through such agencies of regular and chance dispersal as may be available to it.

When we begin with the concept that all species owe their distributional patterns to various aspects of the same set of dynamics, we note that there are wide variations in the size and nature of the area occupied by the different members of the flora. We observe that there appear to be patterns of distribution that relate themselves to various sets of environmental conditions. Some species will appear to be under the influence of certain aspects of climate, such as temperature or moisture.   Other species may seem to be under the influence of edaphic factors, such as the physical conditions of texture or of water-yielding capacity of soil or perhaps some local occurrence of a special metallic ion in the soil solution.   In other cases some aspect of a biotic relationship may prevail.   Were it possible to make a really adequate analysis of such problems we probably would find that almost every conceivable combination of environmental condition could be correlated with the distributional pattern of some species of plant.   It must be emphasized that any environmental factor or combination of factors may be responsible for the restriction of area of some species of plant.   In all probability the environmental relations of the distributional pattern in any given case involve complex interrelationships of several aspects of one or more categories of factors.   Nevertheless, it is also highly probable that in other cases a single aspect of the environment may occur spatially in such a manner as to precisely circumscribe the periphery of the area, or a segment of the periphery of the area, that the species can occupy.   Presumably this condition of the environment at this point spatially represents the limit of tolerance for a vital function, or marks the point where two or more coincident rhythmic cycles cease to be coincidental.   It must be emphasized that the entire periphery of the area occupied by a species is not necessarily under the control of the same factor. An example may be cited in the case of the distributional pattern

of *Sequoia sempervirens* (Lindl.) Dec. Its northward extension
appears to be limited by low winter temperatures, particularly
as these affect seedlings; its eastern boundary coincides with the
boundary of the occurrence of almost daily summer fog; to the
south some other aspect of water relations of soil or atmosphere,
or possibly the oxygen content of the soil solution may be the
limiting factor; to the west it is against the barrier of the Pacific
Ocean; a thirty-mile gap in its range coincides with the occur-
rence of an extensive area of serpentine rock. At many points
along its front any number of minor factors may control the situ-
ation locally. These are different categories of environmental
factors, and for the most part they are critical at different seasons
of the year. In the case of highly restricted patterns of distri-
bution, however, it is more probable that the entire periphery may
be, in most cases, under the control of a single environmental
factor or a single complex of factors. This is especially true
where the limiting factor may be edaphic.

The Edaphic Factor

When we consider the nature of environmental factors whose
various conditions may occupy area independently of the occur-
rence of any species of plant, it seems probable, except for certain
cases of special biotic restriction, that the edaphic factor occurs
spatially in a manner that is most apt to be related to highly
restricted patterns of distribution among plants. The edaphic
factor pertains to the substratum in which plants grow and from
which they derive their mineral nutrition and much of their water
supply. It involves the physical and chemical nature of the sub-
stratum together with the effects of these on the various aspects
of water relations and aeration of soils. Because of the great
local variation that exists in the physical and chemical nature of
the substratum and soils, the edaphic factor presents the possi-
bility of enormous diversity of habitats in any given area. This
diversity is expressive of conditions that may involve presence or
absence, amount, degree of intensity, or rhythmic sequences of
fluctuation of any aspect of the edaphic factor as it may vary from
place to place and from season to season in the area. Because
of the nature of various conditions of the edaphic factor, the geo-
graphic area of the condition is often very sharply delimited.

Edaphic diversity owes its nature to many causes and may
express itself both physically and chemically. Without attempt-
ing to give a complete picture of the causes of this diversity, the
nature of some of it may help to clarify certain aspects of the
problems of highly restricted plants. Most obvious in the cause
of edaphic diversity is variation in the position of the water table.
Where it occurs above the ground level we have lakes, ponds,
pools, and marshes. Its depth below the ground is no less signifi-
cant as an ecological factor. The seasonal fluctuation in the posi-

tion of the water table presents a rhythmic sequence that is very important floristically, especially in arid and semi-arid regions. Where these conditions coincide with particular soil types, special habitats of a highly selective nature are produced. Among these are the vernal pools of the Great Valley of California with their richly endemic floras.

Soils, soil building, and soil leaching provide other aspects of edaphic diversity; here are many forces at work that may produce very local conditions. Soil building and soil maturing, by bringing together and mixing many diverse sediments, tend in some cases to counteract some of the elements of diversity characteristic of certain of the more youthful, highly mineralized situations. Hence, greater floristic diversity sometimes occurs where soils are less mature. Of possible significance to our subject is the ability of certain plants to absorb certain rare earth minerals from the soil and concentrate them in the leaves. When these fall and decay the minerals are deposited in the surface layers of soil in unusual concentrations. It is now an established fact that yttrium is accumulated in unusual quantities in the surface layers of the soil by the disintegration of hickory and walnut leaves (11). Oak leaves from these same localities show no trace of yttrium.

Other causal factors of edaphic diversity are the forces responsible for both epeirogenic and orogenic diastrophism of the earth's crust. Here, through faulting and folding and subsequent wearing down and dissection of the uplifted segments, the various strata of rock become exposed, each with its own physical and chemical features and each producing its own effect on soils. The area and continuity of these outcrops will vary with the thickness of the strata, the length of the exposure, the degree of dissection, and the location of any overburden of soils or soil materials. In highly tilted or highly folded strata the area of some of the outcrops may be exceedingly small. Often all that may remain of a given stratum persists as a cap on the top of a mountain. The contact between strata often is a line of weakness through which water may seep and bring to the surface dissolved minerals, which it deposits in increasing concentration in the surface soils. Faulting and folding often disturb drainage conditions and the movement of water, altering the pattern of erosion and affecting problems of the water table.

The extent of edaphic diversity attendant upon the forces of vulcanism and other igneous agencies is enormous. On the slopes of a single volcano very diverse conditions may result from the nature of the activity and the chemical composition of the magma that wells up. Pyroclastics of various types may be thrown out and roughly sorted into different patterns over the surface, and these may become interbedded or intruded with lavas of various types. The speed of cooling will materially affect the nature of the resultant rock. Lavas filling fissures and forming dykes fre-

quently cause contact metamorphism of the older rock. Super-heated waters, often from great depths, come to the surface charged with compounds of metals or other minerals in solution, which they deposit at the surface. Fumeroles and other solfateric activity persist long after other activity ceases, adding new supplies of mineral substances to the surface layers. Molten lava often is a poor medium for rapid diffusion, and sometimes high concentrations of certain minerals remain local in the hardened lava, often in water-soluble form, resulting in a very diverse pattern of mineral concentration over the surface layer of such a lava flow. Of particular significance to our subject is the role of vulcanism and its attendant phenomena in bringing to the surface many minerals of types both useful and toxic to plants.

Still another cause of great edaphic diversity are the forces attendant upon geological metamorphism. Here significant physical and chemical change is wrought upon rock sometimes on a very wide scale and sometimes quite locally. Where these processes involve substitution, crystallization, and segregation of minerals, the infiltration of waters charged with minerals, and other attendant chemical changes under the influence of heat and pressure, situations are created that may result in very local geographic patterns of edaphic conditions when these rocks become exposed at the surface. Much of the concentration of metals in the earth's crust results from the forces of metamorphism. A great variety of rock type is the result of metamorphism, and it is significant that endemic species of plants are often associated with metamorphics. Outstanding among these rocks are the gneisses, schists, diorites, and serpentines.

Throughout this discussion of the edaphic factor there has been frequent reference to the concentration of minerals and metals in the surface layers of the earth's crust. This aspect of the environment will stand out as very important to anyone studying the problems of restricted distributions of plants, but, unfortunately, there is as yet very little information of a precise nature to enable the subject to be put into clear terms of cause and effect. From the nature of the areas where great concentrations of highly restricted species occur, it appears almost certain that some soil chemicals possess an inordinately high selective value on vegetation. One must not rule out the possibility that they might, in some instances, affect mutation and mutation rate or induce other chromosomal disturbances. Large numbers of restricted species occur on ultrabasic igneous rock and on metamorphics containing metals of the ferro-magnesian complex including in the soil solution (in concentrations often lethal to crop plants) such metals as the ferric irons, magnesium, manganese, chromium, nickel, cobalt, mercury, and most of the other basic heavy metals. Highly restricted endemism on serpentines and serpentinized rock almost the world over provides excellent examples. Here are

variable high concentrations of iron and magnesium and, in some areas, local concentrations of chromium, manganese, nickel, cobalt, and mercury. In some of these areas the sparsity of the flora suggests high toxicity for most of the species readily available to them. The taxonomic peculiarity of the species that do tolerate these conditions suggests that these species, through genetic processes, have been preadapted to these conditions and, hence, that the seed from whence they sprang reached a habitat favorable for them to become successfully established. Gordon and Lipman (4) maintain that the peculiarities of serpentine soils are not due to toxic effects of magnesium, but rather to the unavailability of necessary mineral ions, to high hydrogen-ion concentrations, and to low concentrations of potassium, nitrogen, and phosphorus. Robinson, Edgington, and Byers (12) point to the high toxicity of such substances as chromium, nickel and cobalt, elements which are frequently found in serpentine soils in high concentrations, and attribute to these substances the usual sterility of serpentine soils. Certainly either of these ideas could well account for absence on serpentine soils, but to our subject it is more important that we account for the presence of species that tolerate these substances in such high concentrations. It is these species that make up the endemic element of the floras of such areas.

Foster and San Pedro (2) speculate on the rarity and lack of establishment of seedlings of *Microcycas calocoma* A. DC. in Cuba. It might be relevant to this problem to mention that *Microcycas* occurs in a region where some of the soils derived from chlorite contain the highest concentrations of chromium known in soils (12). Concentrations of from 3.18 to 5.23 per cent of chromic oxide occur locally. This substance is toxic to most plants in concentrations of about 0.1 per cent. Obviously, such soils would be highly sterile to most crop plants and such plants as do occur there can do so only by genetic adjustment of tolerances. Other minerals that seem related to problems of endemism are gypsum (6), diorite, quartzite, and some forms of calcium carbonate. In some instances the effect may be the result of associated minerals or metals not evident to the field observer.

It appears almost certain that some relationship exists between the highly mineralized nature of the substratum and the peculiarities possessed by the floras in such areas, but as yet we are not in a position to state just what that relationship might be. It is a subject that, through newly developed techniques, lends itself to experimental investigation; it is to be hoped that within the near future enough studies of this will be undertaken so that the problem at least can be narrowed down if not solved.

From the standpoint of highly restricted distributional patterns in plants it is important that of all of the environmental influences, the edaphic factor most frequently occurs in sharply de-

fined patterns and often occupies very small areas. It is also important that the toxic substances possessed by certain soils or soil materials may, through restriction or special selection, produce striking vegetational results.

The Misuse of Abstractions

To round out this discussion of the environmental relations of endemism it is desirable to review certain features of previously suggested explanations of the problems of endemism that, to the writer, appear to be based upon fallacious reasoning. Since the time of Engler (1), it has been customary to regard endemics as being of two kinds: first, new species that have not as yet achieved their potential area, and second, relict species that are reduced from a former widespread area. These are two aspects of a single problem, age. Even though a species does possess age as one of its attributes, and even though its distributional pattern does fluctuate through time, no species ever owed its distributional pattern for very long to its age. Old species may be widespread or they may be restricted, they may be abundant or they may be rare. The same may be said of new species after the very brief interval necessary for them to achieve or occupy that portion of their potential area not denied to them by the existence of barriers. In general, each species will occupy locally the same size and configuration of area as do the conditions of the environment to which it is adapted. Age has nothing to do with this. To be sure, the processes that elaborate a species over the available habitats require time, and the longer the species has been in the area the more opportunities it will have had to become genetically elaborated, but it does not necessarily follow that this will happen. Likewise, environmental fluctuation that may serve to restrict or to reduce genetic diversity will vary in rapidity in different areas and in its effect on different species. These processes of distribution and change all require time, but time is not their cause. They may be rapid with one species or infinitely slow or non-existent with others. They may be rapid under one set of conditions and slow under others. These would appear to be individual problems under individual conditions. There is little in this situation to permit generalization as to age, time involved in expanding or receding area, or speed of evolution. Hence, both restricted and widespread species may well be of any age. Age is, therefore, not necessarily a significant attribute of any restricted endemic. Age is sometimes expressible in terms of biotype depauperization, but this need not necessarily imply that the area will be highly restricted or even small. The area that any species of plants may occupy stands as a fact apart from details of its age, so far as cause and effect are concerned.

The phrase "historical factor" is often applied to problems of restricted distribution. This is a vague way of implying that age

is a significant factor or attribute of endemism, as well as being
a phrase with which one may confuse facts attendant upon migra-
tion and establishment with facts pertaining to restriction of
range. There is no doubt that species are characterized by age
and that they have had a history. The history of a plant species
may tell the very important story of *how* it arrived in any given
place and *where* it came from, but it does not explain its persis-
tence nor the precise pattern of the area occupied in the new
environment. The facts pertaining to the pattern of area are tied
up with the individual plants as they are constituted today and
with the environmental conditions as they prevail today. Such
facts are no doubt related to the past, but the past is not the key
to them because it does not necessarily serve to explain them;
nor are they necessarily the key to the past since they are the
result of today's conditions. The term "historical factor" is thus
another abstraction which too often is used without any clear
notion of what it does imply.

Isolation is often referred to as a cause or contributing factor
in endemism. Isolation may explain abstractly the conditions
which operate to preserve or encourage genetic purity by prevent-
ing gene infiltration. It may also aid in maintaining reduced
competition. But since neither isolation nor the condition that
it implies plays a part in bringing the plant into existence or in
preadapting it to the habitat, it cannot of itself initiate any
endemic. In all of these supposed functions isolation is important
for what it implies and not for what it of itself does. The plant
comes into any given habitat as a seed already endowed by genetic
processes with a tolerance range for environmental factors that
determines its capacity to function. Isolation in any given habi-
tat is merely a way of stating that the plant or the species has a
sort of priority to function unmolested by forces that do not exist
in this particular habitat. A factor that does not exist in a habitat
never exercises any influence on the plants of that habitat. Iso-
lation is an abstraction definable only in terms of negative forces.
Neither it nor the absent factors that it implies can be a stimulus
of utility to the functioning of any physiological or genetic
mechanism. At this point the "Sewell Wright effect" (16) may
be adduced to refute my contentions. However, in explaining the
"Sewell Wright effect," isolation is a convenient mode of expres-
sion for what it implies. The significant point in the "Sewell
Wright effect" is the existence of a small population operating
wholly within its own genetic influence.

Because the above difficulties are involved in the concept of
isolation, it becomes very important that facts be kept in their
proper place. This may appear to be trivial quibbling over defi-
nition and concept, but by being precise here we are in a better
position to understand why there is no striking endemism in many
hundreds of isolated islands. In spite of their isolation, coral

islands are notoriously lacking in specific plant endemism. Being essentially alike environmentally, these islands offer little opportunity for environmental selection to operate. Were isolation a causal factor in highly restricted patterns of distribution, there would be no reason why every island should not develop populations of highly restricted species.

Attempts have often been made to correlate the number of endemics in an area with both the size and the age of the area. As for size of area, it is to be expected that there will be correlation in numbers only when there is also relative habitat diversity. Age of area is an abstract expression which implies a complex series of problems involving such features as maturity of terrain, leaching of soils, and time required in genetic processes, all of which may conceivably have some bearing on the problem. But their effect could be completely nullified by lack of environmental diversity. Old land masses are not consistently inhabited by many endemics, and some newly available areas have several. On the other hand, it is conceivable that the factors implied by age of land mass, together with great environmental diversity, might produce numbers of endemics wholly out of proportion to either of these influences alone.

A great deal has been written about area and its significance in the interpretation of the development of vegetation and as a basis for the explanation of various historical trends. Since the plant is adapted through genetic processes to a given set of environmental conditions, the area the plant occupies is purely incidental to the condition to which it is adapted. It occupies this area only because these conditions prevail there. The size and the shape of the area occupied are the product of today's facts, both genetic and environmental. Area as such has no historical significance in vegetation. Thus the concept of "age and area" (15) loses its significance unless it can be established that the condition was expanding its area at a consistent rate or that the mutation rate, or the rate of other genetic phenomena that might enlarge tolerances, was uniform and persistent and was regularly producing types that could persist and expand the area of the species. Likewise, Hultén's idea of equiformal progressive areas (5) does not take these facts into consideration. Since size and shape of the area occupied reflect the occurrence of conditions, any correlation of area with history or historical sequences is strictly coincidental. The important point is that one would of necessity have to establish his historical facts independently of the pattern of distribution of species. The pattern of distribution is determined by causes inherent in the locality and most probably has had no correlative relationship with the history of the flora over any wide area. The type of plant occupying the area (the ecotype) in most instances must have been produced reasonably close to the condition under which it grows. Any species capable

of extensive migration must, by the very nature of things, be exceedingly plastic, that is, it must be very diverse genetically and capable of meeting differing habitats with new ecotypes.

Documentation of some of the ideas herein expressed will follow as Part 2 of this paper in a subsequent number of this journal, wherein the nature and occurrence of concentrations of highly restricted species will be discussed.

Summary of Part 1

1. The dynamics of the geographic distribution of any species involves the interaction between the environment, the physiological processes of the individuals of a population, and the genetic processes that fix tolerances and maintain or elaborate the population and preadapt individuals to environmental fluctuations.

2. Endemic species differ in no significant way from (so-called) "ordinary" species in their dynamics; restriction in geographic range as it applies to endemic species is, therefore, of the same order—so far as cause and effect are concerned—as is the restriction of any and all other species.

3. The area occupied by any species is determined by factors whose various conditions occupy area independently of the fact that species might be restricted by them. Since only environmental conditions independently occupy area, it is the environment that determines the pattern of distribution of all plant species by permitting the functioning of only those individuals whose tolerances have been preadapted to the special conditions of the environment.

4. Of the various categories of environmental factors, the condition of any factor or combination of factors may serve to restrict the range of some species of plants. Of these factors, however, the edaphic factor is most apt to occur in sharply defined patterns and often in small areas. In this connection, the regular occurrence, the world over, of highly restricted species in association with the occurrence of certain minerals and metals in the soil solution, suggests that these substances play an important role in problems of geographic distribution of highly restricted species.

Department of Botany,
University of California, Berkeley.

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A "NEW" CULTIVATED SUNFLOWER FROM MEXICO

Charles B. Heiser, Jr.

The study of the origin of the cultivated sunflower (*Helianthus annuus* L.) is still a relatively unexplored field. *Helianthus annuus* (including *H. lenticularis* Dougl.) is a complex assemblage of weeds of roadsides and city dumps, and of plants cultivated for their seeds or for ornamental purposes. From what is known at present it is assumed that the cultivated sunflower arose from a wild or weed type *H. annuus*.

The sunflower was introduced into Europe in the sixteenth century. In the 1758 edition of Dodonaeus (2) the sunflower is mentioned. The seeds of this plant are stated to be flat and long, and somewhat "browne" or "swarte," and formerly were grown in Spain. Gerard (3) in 1597 describes a sunflower with seeds "black and large," and goes on to describe a second kind of sunflower with the seeds "long and black with certain lines or strakes of white running amongst the same." It is quite probable that the sunflower was first introduced into Europe by the Spanish and that this was a black-seeded variety which in all probability came from Mexico or the southwestern United States. The introduction of the striped variety probably occurred at a later date and this plant may have been introduced from the northern United

States or Canada, where the Indians are known to have cultivated sunflowers. The Mammoth Russian variety, which has reentered this country, probably represents an amalgamation of several races.

FIG. 1.   Achenes of *maiz de teja,* ×2.5.

The earliest description of a cultivated sunflower in Mexico is by Hernández (5), who made his observations during the years 1570–75. Unfortunately neither Hernandez nor any of the other early observers have any reference to the color of the achenes. In 1896 Edward Palmer is reported (7) to have obtained sunflower achenes in Durango, Mexico, and mentioned them as having "a good, plump kernel" and black shells which yield a purplish dye "which is esteemed by some." In the account of the Russian expedition to Mexico in 1925–26, *H. annuus* is recorded as now being cultivated in northern Mexico in limited quantities in maize fields (1). The few samples which were obtained represented late and very late forms, most of which were very tall. Unfortunately a more detailed description is not given.

The finding of a previously unknown cultivated form of sunflower in Teocaltiche, Jalisco, Mexico, by Dr. Carl O. Sauer of the University of California, is of particular interest in this connection. The achenes of this sunflower (text figure 1), called *maiz de teja*[1] by the native from whom they were obtained, were turned over to me for study.

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[1] The name *maiz de Texas* is given by Martínez (6) and *maiz de tejas* by Bukasov (1) for Mexican sunflowers.

These achenes, the large size of which undoubtedly indicates a cultivated strain, are long, narrow, and a shining black. In these respects they resemble to some extent the Hopi cultivated sunflower (4), but they are distinguished readily from the modern

TABLE 1. COMPARISON OF THREE CULTIVATED SUNFLOWERS

CHARACTER	MAIZ DE TEJA	HOPI	MAMMOTH RUSSIAN
achenes			
shape	narrow (with beak)	narrow	broad
color	black	purple	gray striped
hypocotyl			
color	red	red	green
length	long	long	short
stem			
pubescence	scattered hairs	scattered hairs	more densely hairy
leaves			
color	deep green, dull	deep green, shiny	light green, dull
size	small	medium	large
margin	nearly entire	slightly serrate	serrate
decurrence on			
petiole	present	present	usually absent
involucral bracts			
pubescence	medium	light	dense
attenuation	long	short	long to very long
chaff (pales of the			
receptacle)			
color	purple	purple	green
corolla			
color of lobes	deep red	deep red	yellow (rarely red)
shape	narrow	intermediate	broad
bulb of tube	poorly developed with long hairs	well developed, short hairy to glabrate	well developed, densely long hairy
stigma			
color	purple	purple	yellow (rarely red)
hardiness	weak	fairly robust	very robust
maturation	very late	late	early to late

Russian cultivated strains which usually have a plumper seed and never develop such a deep pigmentation. The small beak present on the upper portion of this Mexican achene, however, is an outstanding character and it appears to be unique among the annual sunflowers.

In order to make further comparisons, these and several other lots of sunflowers were grown in an experimental plot at the Missouri Botanical Garden during the summer of 1945. The plants grown from the seed obtained in Teocaltiche were extremely late in maturing and were destroyed by a severe October storm while still in the "bud" stage. All of the other sunflowers growing in the same experimental plot, including a number of modern Russian varieties as well as the Hopi sunflower and weed sunflowers,

had already matured their seed by this time.   It may be signifi-
cant that *maíz de teja* failed to flower in this particular environ-
ment.   Perhaps through long selection *maíz de teja* has become
adapted to a particular set of growing conditions.

During the winter of 1945–46 samples of the Mexican, Hopi,
and Mammoth Russian sunflowers were grown in the greenhouse
of the Division of Genetics, University of California, Berkeley, in
order to study the behavior of the three strains when grown under
presumably identical conditions.   There are still insufficient data
to draw any final conclusions regarding the relation of these three
strains to each other.   The Mexican plants appear to be rather
closely allied to the Hopi plants in a number of characteristics,
the most notable exceptions being the nature of the pubescence
and the attenuation of the involucral bracts.   In the latter charac-
ter the Mexican plants approach the condition found in the Mam-
moth Russian variety.   The Mexican plants again were the last
to mature under greenhouse conditions.   Some of the outstanding
differences and similarities that have been observed thus far in
these three varieties of sunflower are tabulated in Table 1.

The exact relationship of these Mexican sunflowers to the
cultivated sunflower of the Hopi and to the various types culti-
vated in Europe and North America scarcely can be discussed in
the light of the published evidence now available.   Fortunately,
sunflower seeds of various types have been found at different pre-
historic sites in the United States.   When these have been care-
fully surveyed and analyzed the problem will take more definite
shape.   It is also highly desirable that additional information be
obtained on the primitive sunflowers of Mexico.

The author wishes to thank Dr. Edgar Anderson and Dr. Carl
O. Sauer for helpful suggestions and for reading the manuscript.

Department of Botany,
University of California, Berkeley.

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TRIFOLIUM MONANTHUM GRAY

James S. Martin

Some eight entities have been described in the *monanthum* group of *Trifolium* and at least fourteen different combinations have been made. The difficulty of application of these various names is caused by the large degree of intergradation which exists between all possible entities. Although the recognition of the four varieties proposed in the following treatment entails the addition of a new name. the geographical correlation of these four varieties seems to justify such action.

I wish to express my appreciation to the curators of the following herbaria for the loan of material: University of California, Berkeley, California (UC); Dudley Herbarium, Stanford University, California (DH); Pomona College, Claremont, California (P); Gray Herbarium, Harvard University, Cambridge, Massachusetts (G); Missouri Botanical Garden, St. Louis, Missouri (MBG); New York Botanical Garden, New York, New York (NY); Philadelphia Academy of Sciences, Philadelphia, Pennsylvania (PA); Intermountain Herbarium, Utah State Agricultural College, Logan, Utah (IH); and University of Washington, Seattle, Washington (W).

Key to Varieties of Trifolium monanthum

Leaflets of the upper leaves mostly acute, oblanceolate or
  elliptical.
  Plants moderately to strongly villose; peduncles usually
    bent near the top, the inflorescence thus at right
    angles to the peduncles .... d. *T. monanthum* var.
                                                          Eastwoodianum
  Plants glabrous to sparingly villose; inflorescences usu-
    ally erect on straight peduncles .... b. *T. monanthum* var.
                                                          Grantianum
Leaflets of the upper leaves mostly rounded or retuse,
  obcordate to oblanceolate.
  Involucral lobes mostly 0.5–2 mm. long; stems 5–30 cm.
    long; plants usually noticeably villose .... c. *T. monanthum* var.
                                                          parvum
  Involucral lobes mostly more than 2 mm. long, if
    shorter, the stems less than 5 cm. long; plants
    glabrous or sparingly villose .... a. *T. monanthum* var.
                                                          typicum

a. T. monanthum Gray var. typicum nom. nov. *T. monanthum* Gray, Proc. Am. Acad. 6: 523. 1865. *T. monanthum* Gray f. *spatiosum* McDerm., No. Am. Sp. Trifolium 98. 1910 (based on *Hall* and *Chandler 613*, Black Mountain, Fresno County, California, July, 1900, UC; isotypes, MBG, NY, DH).

Glabrous to sparingly villose; stems 1–10 (20) cm. long; leaflets obcordate, obovate, or oblanceolate, rounded, truncate, or retuse at the apex, 2–5 mm. wide, 4–12 mm. long; inflorescences

1–2 (4)-flowered; peduncles usually straight, the flowers erect; involucral lobes 1–5 mm. long; calyx teeth shorter than or about equal to the tube in length.   Flowering from June to August.

Type.   Soda Springs in the Upper Tuolumne Valley, California, June 26, 1863, elevation 8600 feet, *W. H. Brewer 1704* (G; isotypes, UC, DH).

Distribution.   Sierra Nevada from Plumas County to Tulare County, California, east throughout the mountain ranges of Nevada, South Coast Ranges in Ventura and Los Angeles counties, California; along streams and in meadows, 5000 to 11,500 feet elevation.

Representative material.   *W. A. Archer 5468; I. W. Clokey 7562, 7984; V. Duran 3078; R. Ferris 3745, 8960, 8993; A. A. Heller 9306, 10200; C. L. Hitchcock 5462; A. H. Holmgren 1609; B. Maguire 22500, 22547; W. H. Shockley 499.*

The typical variety is best exemplified by material from the region from Mount Rose, Nevada, to Yosemite National Park, California.   Specimens collected from Lake Tahoe to Butte and Plumas counties and in Fresno County, California, and the Charleston Mountains of Nevada are often somewhat intermediate between the typical variety and the varieties *Grantianum* and *Eastwoodianum*.   The leaflets tend to be larger and more nearly acute than those of the typical group and in some cases the calyx teeth are longer, although all are glabrous or very sparingly pubescent.   Some, at least, of these have been referred to *T. monanthum* f. *spatiosum* by McDermott but are not sufficiently different to be so recognized.

b. T. MONANTHUM Gray var. GRANTIANUM (Heller) Parish, Plant World 20 : 220. 1917.   *T. Grantianum* Heller, Muhlenbergia 1 : 136. 1906.   *T. monanthum tenerum* Parish, Bot. Gaz. 38 : 461. 1904, name mistakenly applied.   *T. monanthum* Eastw. *apud* Parish, loc. cit., listed in synonymy.   *T. simulans* House, Bot. Gaz. 41 : 341. 1906 (based on *H. M. Hall 710,* Strawberry Creek, San Jacinto Mountains, California, July 22, 1897; isotypes, G, UC).   *T. monanthum* Gray var. *Grantianum* Zeile *apud* Munz, Man. So. Calif. Bot. 255. 1935.

Glabrous or but sparingly villose; stems 3–30 cm. long; leaflets oblanceolate to obovate or more commonly elliptical, acute (rarely somewhat rounded but then mucronate), spinose-serrate, 2–5 mm. wide, 7–20 mm. long; inflorescences (1) 3–6-flowered, peduncles usually straight, the flowers erect; involucral lobes (1.5) 3–5 (6) mm. long; calyx teeth longer or shorter than the tube.   Flowering from late May to July.

Type.   Mount San Gorgonio, San Bernardino Mountains, California, July 23, 1904, *Geo. B. Grant 6343* (W, no. 79713; isotypes, UC, P, DH).

Distribution.   San Bernardino, San Jacinto, and San Gabriel

mountains of southern California, moist stream banks and mea-
dows, 5000 to 9500 feet elevation.

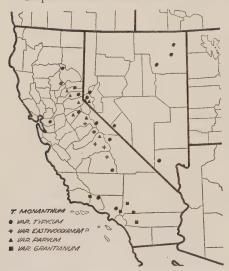Representative material. *V. Duran 3525; H. M. Hall 710, 1812, 2200, 2463, 2552, 7510, 7564, 7571; A. A. Heller 8937; P. A. Munz 6010, 8458, 8610, 8781, 10485, 10486, 10697, 15385; J. Roos 2362.*

T. MONANTHUM
● VAR. TYPICUM
+ VAR. EASTWOODIANUM
▲ VAR. PARVUM
■ VAR. GRANTIANUM

Fig. 1. Distribution of *Trifolium monanthum.*

The variety *Grantianum* occurs only in the mountains of southern California where it is not likely to be mistaken for any other plant. The very acute leaflets are unlike those of any other variety except var. *Eastwoodianum,* a plant which is always much more pubescent and which does not occur south of Tulare County. *T. simulans* House is considered a synonym; isotypes of this species differ from the type of var. *Grantianum* only in being a little larger and in having longer calyx teeth.

c. T. MONANTHUM Gray var. PARVUM (Kell.) McDerm., No. Am. Sp. Trifolium 105. 1910. *T. pauciflorum* Nutt. var. *parvum* Kellogg, Proc. Calif. Acad. Sci. 5: 54. 1873. *T. multicaule* Jones, Bull. Torrey Bot. Club 9: 31. 1882 [based on *M. E. Jones (2592?)*, Soda Springs, Nevada County, California, July 30, 1881 (?), P; isotypes, PA, IH]. *T. parvum* (Kell.) Heller, Muhlenbergia 1: 114. 1905. *T. monanthum* Gray var. *parvum* (Kell.) McDerm. f. *glabrifolium* McDerm., op. cit. 108 (based on *Hall* and *Babcock,* Porcupine Flat, Yosemite National Park, California, July, 1902, UC, no. 33605).

Moderately villose or rarely nearly glabrous; stems 4–30 cm. long; leaflets obovate to oblanceolate, rounded at the apex, serrulate, 2–7 mm. wide, 4–20 mm. long; inflorescences (1) 4–8 (10)-flowered, peduncle usually bent below the inflorescence, the flowers thus more or less at right angles to the peduncle; involucral lobes 0.5–2 (5) mm. long; calyx teeth usually equal to or longer than the tube. Flowering from June to August.

Type. Cisco, Sierra Nevada, California, July 6, 1870, *A. Kellogg* (isotypes, NY, UC).

Distribution. Sierra Nevada from Nevada County to Fresno

County, California, common in meadows, open areas in forest, and along streams, 5000 to 9000 feet elevation.

Representative material.   *H. M. Hall 256, 3385, 3654, 4776, 8737, 8740, 8759, 8775; A. A. Heller 6942, 8986, 9831, 12151, 13296; M. E. Jones 2592.*

This variety is most easily distinguished by the reduced involucres and the usually 4–8-flowered inflorescences which appear to be more or less at right angles to the peduncles.   I have not seen the type but the isotypes represent a depauperate, few-flowered phase.   The more abundant and larger phase with 5–8-flowered inflorescences is represented by the type collection of Jones' *T. multicaule.*

d. T. MONANTHUM Gray var. **Eastwoodianum** nom. nov.   *T. tenerum* Eastwood, Bull. Torrey Bot. Club 29: 81. 1902, not *T. monanthum tenerum* Parish, Bot. Gaz. 38: 461. 1904.

Moderately to rather densely villose; stems 10–35 cm. long; leaflets oblanceolate to elliptical, often very narrowly so, acute, conspicuously spinose-serrate, 2–5 mm. wide, 7–18 mm. long; inflorescences (1) 3–4 (7)-flowered, peduncles usually bent below the inflorescences and the flowers thus seemingly at right angles to the peduncles; involucral lobes (2) 3–4 (5) mm. long; calyx teeth usually a little longer than the tube.   Flowering in July and August.

Type.   Summit, trail to South Fork of King's River, California, July 1–13, 1899, *A. Eastwood* (isotype, UC).

Distribution.   Sierra Nevada from Tuolumne County to Tulare County, California, moist stream banks and meadows, 5000 to 10,000 feet elevation.

Representative material.   *M. S. Baker 4450b; W. R. Dudley 1576, 2094; H. M. Hall 437, 5565; R. Hopping 360; P. A. Munz 7566, 15936.*

This variety is somewhat similar to var. *Grantianum* in respect to leaflet characters but is always conspicuously villose and the inflorescences are usually at right angles to the peduncles.   By these two characters the two varieties can be easily distinguished, especially when considered in connection with their geographical separation.   This variety has been known as *T. monanthum* var. *tenerum* based on a publication by Parish (Bot. Gaz. 38: 461. 1904) in which he gave *T. monanthum* Eastwood (probably intended as *T. tenerum* Eastw.) as the basis for the name and cited two specimens, both of which belong to the variety *Grantianum.* One of the specimens cited is the type collection of *T. monanthum* var. *Grantianum* (Hell.) Parish so that Parish's var. *tenerum* becomes a synonym of var. *Grantianum,* necessitating a new varietal epithet for the entity in question.

Eastern New Mexico College,
Portales, New Mexico.

THE STATUS OF THE SECTION TROPANTHUS GRANT IN MIMULUS OF SCROPHULARIACEAE

H. E. McMinn

Since the earliest attempts by man to classify plants there have been—and there will continue to be—differences of opinion regarding the grouping of plant specimens into named categories such as species, subspecies, genera and sections. These differences of opinion are due to many causes, one of which is the lack of sufficient material for study. This lack of material sometimes leads to misidentification and subsequent wrong classification which often results in the describing of new species. This in itself is a matter of some importance, but when the new species is taken as the type of a new section in a genus, then it becomes a matter of great importance. Such procedure becomes critical when the characters of the new section are used as evidence for breaking down the boundaries of two genera. It is the belief of the writer that one such instance is exemplified by the describing of the species *Mimulus Treleasei* Grant (1, pp. 325–326) and the subsequent establishing of the section *Tropanthus* (1, pp. 324–325) in *Mimulus* of Scrophulariaceae by the same author. Although the section was made in 1924, this writer was not aware of the basis for founding the section until recently when he began a comprehensive study of the genus *Diplacus*.

The section *Tropanthus* was based upon a single specimen of Scrophulariaceae collected at Tehuacan, Mexico, June 2, 1905 (*Wm. Trelease, no. 68,* Missouri Botanical Garden Herbarium no. 112585). The author honored the collector of the specimen by naming it *Mimulus Treleasei* Grant, and stated that, "The type sheet contains only two short branches of this unusual plant, and as this is the only material known it has been impossible to tell anything about the size of the plant nor can the color of the flowers be determined." The author's photograph of the type (1, pl. 3, opposite p. 374), however, only shows a single short branch, not "two short branches." An examination of the type sheet itself (pl. 20, fig. A) shows a single short branch which is undoubtedly the same as that photographed by the author of *Mimulus Treleasei.* Due to this apparent contradiction, one might believe that one branch of the type had been removed when studying the material, but there is no evidence or mention of such removal.

The first impression, as well as later ones gained from more careful study of the type of *Mimulus Treleasei,* led the writer to conclude that the plant was not a *Mimulus,* but that it belonged to the genus *Berendtia* A. Gray (2, p. 379) [*Berendtiella* Wettst. et Harms (4)]. The species appeared to be *Berendtia laevigata* Robins. & Greenm. (3, p. 39) the type of which was collected

PLATE 20. TYPE SPECIMEN OF MIMULUS TRELEASEI (A) AND BERENDTIA
LAEVIGATA (B).

also near Tehuacan, Mexico ("C. G. Pringle, on calcareous ledges near Tehuacan, Puebla, altitude 5,500 feet, 24 December, 1895, no. 6294"). This plant was described in 1896, thirty years before the published date of the new species, *Mimulus Treleasei.* Since the type of *Berendtia laevigata* (pl. 20, fig. B), deposited at the Gray Herbarium and a duplicate of the type deposited at the Missouri Botanical Garden appear to be the same entity as the type of *M. Treleasei,* deposited at the Missouri Botanical Garden, it would seem that Mrs. Grant was not aware of the earlier collection or that she considered the two collections as belonging to different genera. That the two collections are almost identical in their characters is evidence that they belong to the same genus and species. The presence of bractlets on the pedicels of the flowers in both collections is evidence that neither belongs to the genus *Mimulus.*

In the monograph of the genus *Mimulus,* the author of the section *Tropanthus* very definitely attempts to show that *Diplacus* Nutt. should be a section of *Mimulus* L. rather than a distinct genus (1, pp. 114–115). She presents arguments based upon her studies of *Mimulus* to show that all but two of the characters usually used to separate *Diplacus* from *Mimulus* are not valid. These two are "its shrubbiness and peculiar glutinous exudation." As evidence that these characters are not valid, the author presents characters of her newly described species. She states that, *"M. Treleasei,* a newly described species collected by Trelease in the State of Puebla, Mexico, though shrubby and having a glutinous exudation, is not in most of its other characters related to *Diplacus."* She concludes that, "there are then no sufficient characters for maintaining *Diplacus* as a genus" (1, p. 115). The writer is not here particularly concerned as to whether *Diplacus* Nutt. is a genus, but he is concerned by the use of the characters of the section *Tropanthus* to disregard it as such.

In conclusion, it is the opinion of the writer that because the material upon which the section *Tropanthus* is based was wrongly identified, the section is not valid; hence the use of any of its characters as evidence for reducing *Diplacus* Nutt. from a genus to a section of *Mimulus* is not justifiable!

<div style="text-align:right">

Mills College,
Oakland, California.

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REVIEW

American Species of Amelanchier. By GEORGE NEVILLE JONES.
Illinois Biological Monographs, Vol. XX, no. 2. Pp. 1–126.
[Feb.] 1946. The University of Illinois Press, Urbana. $1.50
paper, $2.00 cloth.

This is a detailed account and analysis of some thousands of
herbarium specimens and of the "nearly two hundred binomials
and trinomials representing the species of *Amelanchier* in Amer-
ica." It is well illustrated with fourteen maps and twenty-three
half-tone plates, the latter intended to show the usual leaf-shapes
in the several species and also to illustrate the actual types or type
material of critical entities. The paper is conveniently arranged,
the style and typography are pleasing, the keys and descriptions
are ample, and the citations of literature not only account for all
synonymous names published in the genus but also include a
multitude of references to *Amelanchier* names as used in floras and
manuals and other technical and popular works. As Dr. Jones
mildly says in his introduction, the species of *Amelanchier* are
"sometimes somewhat difficult to distinguish," and his reduction
of all the American members of the genus to eighteen species with
distinctive geographical ranges will be welcomed alike by the
amateur and professional botanist. Included in the paper are
separate keys to flowering and fruiting material, a highly desira-
ble feature in any treatment of a group of plants in which the
individuals in flowering condition bear so little resemblance to the
same plants in fruit and with mature foliage. The treatment of
species is in general conservative, as may be imagined from the
large number recognized by earlier authors but here reduced to
synonymy. The author has gone over the literature on *Amelanchier*
very thoroughly, and has put his species on a firm nomenclatural
basis through study of the types wherever these are known to be
extant.

A few minor errors and imperfections may be noted. What
is evidently intended for a new species, *Amelanchier neglecta,* is
proposed without either Latin description or reference to previous
publication and so is not validly published. Specimens of *Amelan-
chier spicata* are cited from Alabama, but none from Georgia; the
range of the species, as shown in map 7, includes two localities
in Georgia but none in Alabama. In this connection it is worth
noticing that the policy stated on page 12, that of citing only a
part of the collections studied, may lead to confusion on the part
of those using the monograph unless the mapping of ranges and
the selective citation of specimens are carefully coordinated.
Specimens of *Amelanchier laevis,* for example, are cited from
Georgia from the extreme northern counties only. Map 4, how-
ever, indicates that the southernmost limit of this essentially
Appalachian species is much further south, evidently well within

the limits of the Coastal Plain. On page 47 are cited specimens of *Amelanchier canadensis* collected at Franklin, Georgia, but map 6 does not indicate this extension of range; it shows instead a locality which is apparently near Rome, Georgia, a northwesterly range-extension which is not referred to in the citation of specimens.

An improvement might have been brought about in the paper by the inclusion of data obtained from several of the smaller, regional herbaria which have rich local collections, particularly in the southeastern United States and in the Rocky Mountain– Great Basin region. Where critical entities are involved, and especially when herbarium material from some areas is not generally available in large amounts in most collections, it seems unwise to lean so heavily on so few herbaria, even if they be as inclusive as those of Harvard University.

A change for the better might have been made in the lists of specimens examined, by citing county names in addition to the bare collectors' localities or, if space was at a premium, by citing the county names instead of the specific localities, at least for the eastern states. On page 56, for example, are cited specimens collected by [F. J.] Hermann at Portage Lake, Michigan. It so happens that this is not the large and well known Portage Lake in Houghton County, nor the smaller lake of the same name in Crawford County, but a still smaller body of water, omitted from ordinary maps, in Washtenaw County.

Most of us who have studied *Amelanchier* in the field and in the herbarium will agree that the number of species is relatively small. Unfortunately no one up to the present time has been able to explain clearly how to separate some of the critical species from their close relatives. It seems to me that this is the major fault of this monograph, that the author still does not offer convincing criteria by which the critical species may be delimited. *Amelanchier alnifolia* Nutt., for example, as defined by Dr. Jones, is common and widely distributed from Colorado and North Dakota westward and northwestward. *Amelanchier pumila* Nutt., which is dotted sparingly through a part of the same range, is distinguished in the keys on the sole basis of its complete lack of pubescence. Quite possibly it may be a valid species, and not merely a glabrous form of *A. alnifolia,* but from the descriptions and the photograph of Nuttall's specimen of *A. pumila* (Pl. IX, f. 2) it is evident that it is not very different from *A. alnifolia,* which is *almost* instead of *completely* glabrous; this hardly seems a convincing character on which to maintain a species.

An equivalent situation obtains in the northern Great Basin, particularly in northern and western Nevada, where a common *Amelanchier* has the permanently puberulent foliage of *A. utahensis* but the glabrous twigs and five styles of *A. alnifolia,* which is said not to occur in Nevada. Perhaps the two species are less sharply

separated in nature than the monograph would have us believe, or
perhaps certain characters of pubescence and reduction in num-
ber of flower parts have been overemphasized.   The obvious simi-
larities which link all the amelanchiers of western North America
seem far more worthy of recognition than do the rather trivial
morphological differences among them.   The author of this
paper has chosen to take a positive stand by defining as species
certain populations which are, truly enough, rather easily recog-
nized and more or less geographically regionalized.   These popu-
lations, however, are by no means always (or even often) to be
sharply delimited; they may equally well be regarded as varieties
or subspecies or ecospecies or some other units of a single highly
variable species or, on the other hand, be divided into a score of
species.   If one is to establish what are essentially arbitrary limits
for the species he has decided upon in this group, he must offer
considerable justification for such a course.

In the introduction to this monograph the possibility of exten-
sive hybridization in *Amelanchier* is dismissed rather impatiently.
Presumably this is a subject for judgment by a geneticist, but
even to a lay observer there are suggestions of hybridity in some
groups of the genus.   In the Maryland woods here at the edge
of the Coastal Plain there are apparently two species of shrubby ·
amelanchiers with small flowers.   One is a low shrub flowering
perhaps a week before its somewhat larger associate.   According
to Jones' key it is evident that these plants must be either *A. cana-
densis* or *A. spicata*.   Unfortunately not all plants fall clearly into
one species or the other.   In a random selection from a series of
shrubs may be found all possible combinations of the characters
of style-fusion and ovary-pubescence used in the key.   Very
probably the plants really represent two species, but if so their
distinctive characters seem to have become rather tangled.   Un-
like the "species" of western North America, many of these plants
of the eastern states are distinctive in habit and appearance as
well as in flowering season, and apparently this is not a case of
intergrading populations but of different plants which have been
insufficiently studied.

In the same patch of woods mentioned above are numerous
plants of the large-flowered amelanchiers which are truly arbores-
cent.   Some are woolly-leaved while in flower (a character of *A.
arborea*) while others have reddish and almost glabrous leaves (as
in *A. laevis*).   The broad sepals of *A. arborea,* however, may be
found associated with either type of pubescence, as may the gla-
brous racemes of *A. laevis*.   It is not at all clear from examination
of these individuals whether *A. arborea* and *A. laevis* represent two
species, or simply races of one and the same species, or whether
the puzzling intermediates have resulted from hybridization or in
some other manner.

The two preceding examples are enough to suggest, at least,

that we know too little about the genetical behavior of *Amelan-chier*. Perhaps the problems involved are insoluble, but at least they deserve consideration. The members of the Rosaceae, including the Pomoideae, are noted for their sexual irregularities and other reproductive anomalies. Whether due to hybridism, peculiar chromosome distribution, polyploidy, or parthenogenesis, to combinations of these, or to other factors, the multiplicity of forms in *Amelanchier* (as also in *Crataegus, Malus, Rubus* and other genera), is so great as to defy taxonomy based on herbarium material alone. I think we shall not arrive at any very satisfactory scheme of classification of these genera until we know more about their genetical peculiarities. Studies of these will not be easy, for, in growing these long-lived woody species, mature fertile seedlings of known parentage are not quickly obtained, but experimental studies of seedling populations should without fail form the basis of any future attempts to reduce the species of the Pomoideae to a tangible system. The present monograph will serve as a morphological and geographical basis for future work on *Amelanchier*.—Rogers McVaugh, Plant Industry Station, U. S. Department of Agriculture, Beltsville, Maryland.

NOTES AND NEWS

Dr. G. L. Stebbins, Jr., Associate Professor of Genetics, University of California, Berkeley, is absent on sabbatical leave until January, 1947. During the autumn he will deliver the Jessup Lectures on Evolution at Columbia University. These lectures will be published subsequently in book form.

As a member of an expedition sent out under the auspices of the United States Commercial Corporation, Dr. F. Ray Fosberg is exploring for plants in Micronesia.

At the invitation of the Ministerio de Educacion Nacional de Colombia, T. Harper Goodspeed, Professor of Botany, University of California, Berkeley, left on July 4 to give a series of lectures at Bogotá and Medellín. He will return to Berkeley in time for the fall semester.

The following recent appointments have come to our attention: Daniel I. Axelrod as Assistant Professor of Geology, University of California, Los Angeles; Charles B. Heiser, Jr., as Instructor in Botany, University of California, Davis; John L. Morrison as Instructor in Botany, New York State College of Forestry, Syracuse University, New York; Robert M. Muir as Instructor in Botany at Pomona College, Claremont, California.